# The Effect of Delay on a Diffusive Predator-Prey System with Holling Type-li Predator Functional Response 

Shanshan Chen<br>Junjie Wei<br>Junping Shi<br>William \& Mary, jxshix@wm.edu

Follow this and additional works at: https://scholarworks.wm.edu/aspubs

## Recommended Citation

Chen, S., Shi, J., \& Wei, J. (2013). The effect of delay on a diffusive predator-prey system with Holling typeII predator functional response. Communications on pure and applied analysis, 12(1), 481-501.

This Article is brought to you for free and open access by the Arts and Sciences at W\&M ScholarWorks. It has been accepted for inclusion in Arts \& Sciences Articles by an authorized administrator of W\&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

# THE EFFECT OF DELAY ON A DIFFUSIVE PREDATOR-PREY SYSTEM WITH HOLLING TYPE-II PREDATOR FUNCTIONAL RESPONSE 

Shanshan Chen<br>Department of Mathematics, Harbin Institute of Technology Harbin, Heilongjiang, 150001, P.R. China<br>and<br>Department of Mathematics, College of William and Mary Williamsburg, Virginia 23187, USA<br>Junping Shi<br>Department of Mathematics, College of William and Mary Williamsburg, Virginia 23187, USA<br>Junjie Wei ${ }^{1}$<br>Department of Mathematics, Harbin Institute of Technology Harbin, Heilongjiang, 150001, P.R. China

> (Communicated by Xingfu Zou)


#### Abstract

A delayed diffusive predator-prey system with Holling type-II predator functional response subject to Neumann boundary conditions is considered here. The stability/instability of nonnegative equilibria and associated Hopf bifurcation are investigated by analyzing the characteristic equations. By the theory of normal form and center manifold, an explicit formula for determining the stability and direction of periodic solution bifurcating from Hopf bifurcation is derived.


1. Introduction. A diffusive predator-prey system with Holling type-II functional response [9] is a prototypical reaction-diffusion model describing a pair of species with consumer-resource interaction [15, 26]. The equation is in the form

$$
\begin{cases}\frac{\partial u}{\partial t}-d_{1} \Delta u=u\left(1-\frac{u}{k}\right)-\frac{m u v}{u+1}, & x \in \Omega, t>0  \tag{1.1}\\ \frac{\partial v}{\partial t}-d_{2} \Delta v=-r v+\frac{m u v}{u+1}, & x \in \Omega, t>0 \\ \partial_{\nu} u=\partial_{\nu} v=0, & x \in \partial \Omega, t>0 \\ u(x, 0)=u_{0}(x) \geq 0, v(x, 0)=v_{0}(x) \geq 0, & x \in \Omega\end{cases}
$$

Here $\Omega$ is a bounded domain in $\mathbb{R}^{N}, N \geq 1$, with a smooth boundary $\partial \Omega ; \nu$ is the outward unit normal vector on $\partial \Omega ; u(x, t)$ and $v(x, t)$ are the densities of the prey and predator at time $t>0$ and a spatial position $x \in \Omega$ respectively; $d_{1}, d_{2}>0$

[^0]are the diffusion coefficients of the species; $k>0$ is the carrying capacity of prey; $r>0$ is the mortality rate of predator; $m>0$ is the measure of the interaction strength between two species. This reaction-diffusion model (1.1) has been widely used in ecological and biological applications (see e.g. [14, 15, 17]). More biological explanation of this predator-prey system can be found in [15, 26].

System (1.1) has been analyzed or simulated by some researchers. Medvinsky et.al. [15] showed that (1.1) possesses a rich structure of spatiotemporal dynamics through extensive numerical simulations. In [26], Yi, Wei and Shi investigated the bifurcations of non-constant equilibria and periodic orbits of (1.1) with parameter $\beta$, and they obtained that in some situations spatially nonhomogeneous periodic orbits and nonhomogeneous steady state solutions exist in (1.1). Peng and Shi [16] gave some further results on the steady state solutions, that is when $m$ is sufficient large, system (1.1) had no nonconstant positive steady state solutions. System (1.1) was also considered in [12].

Time-delay in some interactions of an evolution system may have significant impact on the underlying dynamics. Hence reaction-diffusion systems with time delays have been proposed as models for the population ecology and biology in recent years (see $[3,6,10,11,19,20,21,24,25]$ ). There are many results of various delayed diffusive predator-prey systems, regarding bifurcations at equilibria, and local/global stability of the constant equilibrium (see e.g. [3, 10, 19, 21, 24, 25] and references therein). As for predator-prey systems, the delay effect on the growth rate per capita of predator or prey is often considered (see [10, 23, 27]). In this paper we consider the delay effect on the growth rate per capita of predator, then system (1.1) becomes

$$
\begin{cases}\frac{\partial u}{\partial t}-d_{1} \Delta u=u\left(1-\frac{u}{k}\right)-\frac{m u v}{u+1}, & x \in \Omega, t>0  \tag{1.2}\\ \frac{\partial v}{\partial t}-d_{2} \Delta v=-r v+\frac{m u(t-\tau) v}{u(t-\tau)+1}, & x \in \Omega, t>0 \\ \partial_{\nu} u=\partial_{\nu} v=0, & x \in \partial \Omega, t>0 \\ u(x, t)=u_{0}(x, t) \geq 0, v(x, t)=v_{0}(x, t) \geq 0, & x \in \Omega, t \in[-\tau, 0]\end{cases}
$$

where $\tau \geq 0$ represents the delay effect on growth rate per capita of predator.
System (1.2) has three nonnegative constant equilibria $(0,0),(k, 0)$ and $\left(\beta, v_{\beta}\right)$, where

$$
\begin{equation*}
\beta=\frac{r}{m-r}, v_{\beta}=\frac{(k-\beta)(1+\beta)}{k m} \tag{1.3}
\end{equation*}
$$

when $m>\frac{(1+k) r}{k}$ (or equivalently $0<\beta<k$ ), and only two nonnegative constant equilibria $(0,0)$ and $(k, 0)$ when $0<m \leq \frac{(1+k) r}{k}$. In the following we use $\beta$ as a bifurcation parameter. In [26], it was shown that when the parameters $\beta$ and $k$ satisfy
(i) $k>1$ and $(k-1) / 2 \leq \beta<k$; or
(ii) $0<k \leq 1$ and $0<\beta<k$,
the positive equilibrium $\left(\beta, v_{\beta}\right)$ is locally asymptotically stable with respect to the dynamics of (1.1), or equivalently the one for (1.2) with $\tau=0$. In the case of (i), $\beta=(k-1) / 2$ is a Hopf bifurcation point for (1.1) so that a stable oscillatory pattern emerges for $\beta<(k-1) / 2$. In this paper, our main result is that under (i), the positive equilibrium $\left(\beta, v_{\beta}\right)$ will lose its stability with respect to the dynamics of (1.2) for a large delay $\tau$. More precisely, we show that there is a strictly increasing function $\tau_{0}^{0}(\beta)$ defined for $(k-1) / 2 \leq \beta<k$ satisfying $\tau_{0}^{0}((k-1) / 2)=0$ and
$\lim _{\beta \rightarrow k} \tau_{0}^{0}(\beta)=\infty$, so that for $(k-1) / 2<\beta<k,\left(\beta, v_{\beta}\right)$ is locally asymptotically stable for $\tau<\tau_{0}^{0}(\beta)$, and it is unstable for $\tau>\tau_{0}^{0}(\beta)$. Moreover a Hopf bifurcation occurs at $\tau=\tau_{0}^{0}(\beta)$ so the constant equilibrium loses the stability to a spatially homogenous periodic orbit. For the case of (ii), we have similar results.

Our result shows that a stable oscillatory pattern in (1.2) can be induced by either a larger delay $\tau$ or a smaller $\beta$, hence a combined impact of the delay $\tau$, the interaction strength $m$ and the predator mortality rate $r$ can destabilize the positive equilibrium state so the system (1.2) exhibits oscillatory behavior. Such delay-induced Hopf bifurcations occur in (1.2) for all the $\beta$ values for which $\left(\beta, v_{\beta}\right)$ is locally asymptotically stable for system (1.1). This is different from a similar diffusive Leslie-Gower predator-prey system [1] studied by the authors recently, in which the global stability of the constant equilibrium persists for all delay values $\tau>0$. For system (1.2), it is not known whether or not $\left(\beta, v_{\beta}\right)$ can be globally asymptotically stable when $\tau>0$, although the global stability of $\left(\beta, v_{\beta}\right)$ when $\tau=0$ can be established by a Lyapunov functional for $k-1<\beta<k$ (see [26]).

The rest of this paper is organized as follows. In Section 2, we analyze the stability/instability of nonnegative equilibria of system (1.2) through the study of associated characteristic equations and show the occurrence of Hopf bifurcation at the positive equilibrium $\left(\beta, v_{\beta}\right)$. We also give a detailed description of the distribution of the characteristic values of the associated characteristic equations of $\left(\beta, v_{\beta}\right)$. In Section 3, we investigate the stability and direction of bifurcating periodic orbits by using normal form $[8,22]$ and the center manifold theorem due to Lin, So and Wu [13]. Some numerical simulations are also presented in Section 3. Throughout the paper, we denote by $\mathbb{N}_{0}$ the set of all the nonnegative integers and $\mathbb{R}^{+}$the set of all the positive real numbers.
2. Stability analysis of equilibria and bifurcation. In this section, we consider system (1.2) on the spatial domain $\Omega=(0, l \pi)$, with $l \in \mathbb{R}^{+}$,

$$
\begin{cases}\frac{\partial u}{\partial t}-d_{1} \frac{\partial^{2} u}{\partial x^{2}}=u\left(1-\frac{u}{k}\right)-\frac{m u v}{u+1}, & x \in(0, l \pi), t>0  \tag{2.1}\\ \frac{\partial v}{\partial t}-d_{2} \frac{\partial^{2} v}{\partial x^{2}}=-r v+\frac{m u(t-\tau) v}{u(t-\tau)+1}, & x \in(0, l \pi), t>0 \\ \frac{\partial u(x, t)}{\partial x}=\frac{\partial v(x, t)}{\partial x}=0, & x=0, l \pi, t>0 \\ u(x, t)=u_{0}(x, t) \geq 0, v(x, t)=v_{0}(x, t) \geq 0, & x \in[0, l \pi], t \in[-\tau, 0]\end{cases}
$$

In this section, we assume that $m>\frac{(1+k) r}{k}$, then system (2.1) has three nonnegative equilibria $(0,0),(k, 0)$ and $\left(\beta, v_{\beta}\right)$ (defined in (1.3)). It is easy to show that the equilibria $(0,0)$ and $(k, 0)$ are unstable with respect to the ODE dynamics, hence they are also unstable with respect to (2.1). In the remaining part of this section, we shall analyze the stability/instability of positive constant equilibrium $\left(\beta, v_{\beta}\right)$.

Since we use $\beta$ as the bifurcation parameter, we substitute $m=\frac{r}{\beta}+r$ into system (2.1). Note that if $m>\frac{(1+k) r}{k}$, then $0<\beta<k$. Transforming the positive equilibrium $\left(\beta, v_{\beta}\right)$ to the origin via the translation $\hat{u}=u-\beta, \hat{v}=v-v_{\beta}$ and
dropping the hats for simplicity of notation, then we have

$$
\begin{cases}u_{t}-d_{1} u_{x x}=(u+\beta)\left(1-\frac{u+\beta}{k}-\frac{r(\beta+1)\left(v+v_{\beta}\right)}{\beta(u+\beta+1)}\right), & x \in(0, l \pi), t>0  \tag{2.2}\\ v_{t}-d_{2} v_{x x}=-r\left(v+v_{\beta}\right)+\left(\frac{r}{\beta}+r\right) \frac{\left(u_{\tau}+\beta\right)\left(v+v_{\beta}\right)}{u_{\tau}+\beta+1}, & x \in(0, l \pi), t>0 \\ \frac{\partial u(x, t)}{\partial x}=\frac{\partial v(x, t)}{\partial x}=0, & x=0, l \pi, t>0\end{cases}
$$

where $u=u(x, t), u_{\tau}=u(x, t-\tau), v=v(x, t)$. Denote $X=C\left([0, l \pi], \mathbb{R}^{2}\right)$. In the abstract space $C([-\tau, 0], X)$, system (2.2) can be regarded as the following abstract functional differential equation

$$
\begin{equation*}
\frac{d U(t)}{d t}=d \Delta U(t)+L\left(U_{t}\right)+F\left(U_{t}\right) \tag{2.3}
\end{equation*}
$$

where $d \Delta=\left(d_{1} \Delta, d_{2} \Delta\right)$,

$$
\operatorname{dom}(d \Delta)=\left\{(u, v)^{T}: u, v \in C^{2}([0, l \pi], \mathbb{R}), u_{x}, v_{x}=0, x=0, l \pi\right\}
$$

and $L: C([-\tau, 0], X) \rightarrow X, F: C([-\tau, 0], X) \rightarrow X$ are given by

$$
L(\phi)=\binom{\frac{\beta(k-1-2 \beta)}{k(1+\beta)} \phi_{1}(0)-r \phi_{2}(0)}{\frac{k-\beta}{k(\beta+1)} \phi_{1}(-\tau)}, \quad F(\phi)=\binom{F_{1}(\phi)}{F_{2}(\phi)}
$$

for $\phi=\left(\phi_{1}, \phi_{2}\right)^{T} \in C([-\tau, 0], X)$, where

$$
\begin{aligned}
F_{1}(\phi)= & \frac{(k-\beta)}{k(1+\beta)} \phi_{1}(0)+r \phi_{2}(0)+\beta-\frac{\beta^{2}+\phi_{1}^{2}(0)}{k} \\
& -\left(\frac{r}{\beta}+r\right) \frac{\left(\phi_{1}(0)+\beta\right)\left(\phi_{2}(0)+v_{\beta}\right)}{\phi_{1}(0)+\beta+1} \\
F_{2}(\phi)= & -\frac{(k-\beta)}{k(1+\beta)} \phi_{1}(-\tau)-r \phi_{2}(0)-r v_{\beta} \\
& +\left(\frac{r}{\beta}+r\right) \frac{\left(\phi_{1}(-\tau)+\beta\right)\left(\phi_{2}(-\tau)+v_{\beta}\right)}{\phi_{1}(-\tau)+\beta+1} .
\end{aligned}
$$

Then the linearization of system (2.2) near $\left(\beta, v_{\beta}\right)$ is

$$
\begin{equation*}
\frac{d U(t)}{d t}=d \Delta U(t)+L\left(U_{t}\right) \tag{2.4}
\end{equation*}
$$

From Wu [22], we obtain that the characteristic equation for the linearized system (2.4) is

$$
\begin{equation*}
\lambda y-d \Delta y-L\left(e^{\lambda} y\right)=0, \quad y \in \operatorname{dom}(d \Delta), \quad y \neq 0 \tag{2.5}
\end{equation*}
$$

It is well known that the eigenvalue problem

$$
-\psi^{\prime \prime}=\mu \psi, x \in(0, l \pi), \psi^{\prime}(0)=\psi^{\prime}(l \pi)=0
$$

has eigenvalues $\mu_{n}=\frac{n^{2}}{l^{2}},(n=0,1,2, \cdots)$, with the corresponding eigenfunctions $\psi_{n}(x)=\cos \frac{n}{l} x$. Substituting

$$
y=\sum_{n=0}^{\infty} \cos \frac{n}{l} x\binom{y_{1 n}}{y_{2 n}}
$$

into characteristic equation (2.5), we obtain

$$
\left(\begin{array}{cc}
\frac{\beta(k-1-2 \beta)}{k(1+\beta)}-\frac{d_{1} n^{2}}{l^{2}} & -r \\
\frac{(k-\beta)}{k(\beta+1)} e^{-\lambda \tau} & -\frac{d_{2} n^{2}}{l^{2}}
\end{array}\right)\binom{y_{1 n}}{y_{2 n}}=\lambda\binom{y_{1 n}}{y_{2 n}}, n=0,1,2, \cdots
$$

Therefore the characteristic equation (2.5) is equivalent to

$$
\begin{equation*}
\Delta_{n}(\lambda, \tau)=\lambda^{2}+A_{n} \lambda+B_{n}+C e^{-\lambda \tau}=0, \quad n=0,1,2, \cdots \tag{n}
\end{equation*}
$$

where

$$
\begin{gathered}
A_{n}=\frac{\left(d_{1}+d_{2}\right) n^{2}}{l^{2}}-\frac{\beta(k-1-2 \beta)}{k(1+\beta)} \\
B_{n}=\frac{d_{1} d_{2} n^{4}}{l^{4}}-\frac{d_{2} n^{2}}{l^{2}} \frac{\beta(k-1-2 \beta)}{k(1+\beta)} \\
\quad C=\frac{r(k-\beta)}{k(\beta+1)}
\end{gathered}
$$

The stability/instability of positive equilibrium $\left(\beta, v_{\beta}\right)$ can be determined by the distribution of the roots of Eqs. $\left(2.5_{n}\right), n=0,1,2, \cdots$, that is, the equilibrium $\left(\beta, v_{\beta}\right)$ is locally asymptotically stable if all the roots of Eqs. $\left(2.5_{n}\right), n=0,1,2, \cdots$ have negative real parts. From the result of Ruan and Wei [18, Corollary 2.4], the sum of the multiplicities of the roots of Eq. $\left(2.5_{n}\right)$ in the open right half plane changes only if a root appears on or crosses the imaginary axis.

In the following, fixing parameters $d_{1}, d_{2}, k, r, l$ in (2.2), we use $\tau$ as the main bifurcation parameter while the value of $\beta$ may vary in different places. It can be verified that if $0<k \leq 1$, then 0 is not a root of Eqs. $\left(2.5_{n}\right), n=0,1,2, \cdots$, when $\beta \in(0, k)$, and if $k>1$, then 0 is not a root of Eqs. $\left(2.5_{n}\right), n=0,1,2, \cdots$, when $\beta \in[(k-1) / 2, k)$.

If $\pm i \sigma(\sigma>0)$ is a pair of roots of Eq. $\left(2.5_{n}\right)$, then we have

$$
\left\{\begin{array}{l}
\sigma^{2}-B_{n}=C \cos \sigma \tau,  \tag{n}\\
\sigma A_{n}=C \sin \sigma \tau,
\end{array} \quad n=0,1,2, \cdots,\right.
$$

which leads to

$$
\begin{equation*}
\sigma^{4}+\left(A_{n}^{2}-2 B_{n}\right) \sigma^{2}+B_{n}^{2}-C^{2}=0, \quad n=0,1,2, \cdots \tag{n}
\end{equation*}
$$

where

$$
\begin{align*}
& A_{n}^{2}-2 B_{n}=\frac{d_{2}^{2} n^{4}}{l^{4}}+\left(\frac{d_{1} n^{2}}{l^{2}}-\frac{\beta(k-1-2 \beta)}{k(1+\beta)}\right)^{2} \\
& B_{n}^{2}-C^{2}=\frac{d_{2}^{2} n^{4}}{l^{4}}\left(\frac{d_{1} n^{2}}{l^{2}}-\frac{\beta(k-1-2 \beta)}{k(1+\beta)}\right)^{2}-\frac{r^{2}(k-\beta)^{2}}{k^{2}(\beta+1)^{2}} \tag{2.8}
\end{align*}
$$

Since $\lim _{n \rightarrow \infty}\left(B_{n}^{2}-C^{2}\right)=+\infty$ for any $0<\beta<k$, then there exists a minimal $N_{0}(\beta) \geq 0$ such that Eq. $\left(2.7_{n}\right)$ has no positive root for $n>N_{0}(\beta)$ and Eq. (2.7 $\left.n_{n}\right)$ has one positive root at most for $0 \leq n \leq N_{0}(\beta)$.

For $0 \leq n \leq N_{0}(\beta)$, if Eq. $\left(2.7_{n}\right)$ has a positive root $\sigma_{n}$ satisfying

$$
\begin{equation*}
\sigma_{n}^{2}=\frac{-\left(A_{n}^{2}-2 B_{n}\right)+\sqrt{\left(A_{n}^{2}-2 B_{n}\right)^{2}-4\left(B_{n}^{2}-C^{2}\right)}}{2} \tag{2.9}
\end{equation*}
$$

then Eq. $\left(2.5_{n}\right)$ has a pair of imaginary roots $\pm i \sigma_{n}$ when

$$
\begin{equation*}
\tau=\tau_{n}^{j}=\tau_{n}^{0}+\frac{2 j \pi}{\sigma_{n}}, \quad j=0,1,2, \cdots \tag{2.10}
\end{equation*}
$$

where $\tau_{n}^{0}$ satisfies

$$
\tau_{n}^{0}= \begin{cases}\frac{\arccos \frac{\sigma_{n}^{2}-B_{n}}{C}}{\sigma_{n}}, & \text { if } A_{n} \geq 0  \tag{2.11}\\ \frac{2 \pi-\arccos \frac{\sigma_{n}^{2}-B_{n}}{C}}{\sigma_{n}}, & \text { if } A_{n}<0\end{cases}
$$

From dependence of $A_{n}, B_{n}$ and $C$ on $\beta, \tau_{n}^{j}=\tau_{n}^{j}(\beta)$ can be regarded as a function of $\beta$. Let $N=\max _{0<\beta<k} N_{0}(\beta)$. Here we give some properties of curves $\tau=\tau_{n}^{j}(\beta)$, for $0 \leq n \leq N, j \in \mathbb{N}_{0}$.

Lemma 2.1. Denote by $\mathcal{D}_{n}$ the domain of $\tau=\tau_{n}^{j}(\beta), 0 \leq n \leq N$ and $j \in \mathbb{N}_{0}$. Then

$$
\begin{equation*}
\mathcal{D}_{n}=\left\{\beta: 0<\beta<k, B_{n}^{2}-C^{2}<0\right\} . \tag{2.12}
\end{equation*}
$$

Proof. From Eq. (2.11), we know that $\tau_{n}^{0}(\beta)$ is the minimal positive $\tau$-value for Eq. $\left(2.5_{n}\right)$ possessing a couple of purely imaginary roots. Eq. $\left(2.5_{n}\right)$ has a couple of purely imaginary roots if and only if Eq. $\left(2.7_{n}\right)$ has a positive root. Since $A_{n}^{2}-2 B_{n}$ is always nonnegative, Eq. $\left(2.5_{n}\right)$ has a couple of purely imaginary roots if and only if $B_{n}^{2}-C^{2}<0$. Then we obtain that the domain of $\tau_{n}^{0}(\beta)$ is

$$
\mathcal{D}_{n}=\left\{\beta: 0<\beta<k, B_{n}^{2}-C^{2}<0\right\}, 0 \leq n \leq N
$$

Since the domain of $\tau_{n}^{j}(\beta)$ is same as that of $\tau_{n}^{0}(\beta)$ when $j \geq 1$, then the domain of $\tau_{n}^{j}(\beta)$ is also $\mathcal{D}_{n}$ for $j \geq 1$.

Let $\lambda_{n}(\tau)=\gamma_{n}(\tau)+i \sigma_{n}(\tau)$ be the root of Eq. $\left(2.5_{n}\right)$ satisfying $\gamma_{n}\left(\tau_{n}^{j}\right)=0$ and $\sigma_{n}\left(\tau_{n}^{j}\right)=\sigma_{n}$ when $\tau$ is close to $\tau_{n}^{j}$. Then we have the following transversality condition.

Lemma 2.2. $\gamma_{n}^{\prime}\left(\tau_{n}^{j}(\beta)\right)>0$, for $\beta \in \mathcal{D}_{n}, 0 \leq n \leq N$, and $j \in \mathbb{N}_{0}$.
Proof. Substituting $\lambda_{n}(\tau)$ into Eq. $\left(2.5_{n}\right)$ and taking the derivatives with respect to $\tau$ yields

$$
\begin{aligned}
{\left[\left.\frac{d \gamma_{n}}{d \tau}\right|_{\tau=\tau_{n}^{j}}\right]^{-1} } & =\operatorname{Re}\left[\left.\left(\frac{2 e^{\lambda \tau}}{C}+\frac{A_{n} e^{\lambda \tau}}{C \lambda}-\frac{\tau}{\lambda}\right)\right|_{\tau=\tau_{n}^{j}}\right] \\
& =\frac{2 \cos \sigma_{n} \tau_{n}^{j}}{C}+\frac{A_{n} \sin \sigma_{n} \tau_{n}^{j}}{C \sigma_{n}}
\end{aligned}
$$

Since $\sigma_{n}$ and $\tau_{n}^{j}$ satisfy $\sigma_{n}^{2}-B_{n}=C \cos \sigma_{n} \tau_{n}^{j}$ and $\sigma_{n} A_{n}=C \sin \sigma_{n} \tau_{n}^{j}$, and from the expression of $\sigma_{n}^{2}$ in (2.9), then we have

$$
\begin{aligned}
{\left[\left.\frac{d \gamma_{n}}{d \tau}\right|_{\tau=\tau_{n}^{j}}\right]^{-1} } & =\frac{2 \sigma_{n}^{2}-2 B_{n}}{C^{2}}+\frac{A_{n}^{2}}{C^{2}} \\
& =\frac{\sqrt{\left(A_{n}^{2}-2 B_{n}\right)^{2}-4 B_{n}^{2}+4 C^{2}}}{C^{2}}
\end{aligned}
$$

Therefore $\gamma_{n}^{\prime}\left(\tau_{n}^{j}\right)>0$.

It is clear from (2.10) that $\tau_{n}^{j+1}(\beta)>\tau_{n}^{j}(\beta)$, and the following proposition show that $\tau_{n+1}^{j}(\beta)>\tau_{n}^{j}(\beta)$, hence we have a complete ordering of the bifurcation values $\tau_{n}^{j}(\beta)$.

Proposition 2.3. $\operatorname{Let} \tau_{n}^{j}(\beta)$ be defined as in (2.10) and (2.11).

1. If $k>1$, then for any $\beta \in[(k-1) / 2, k), \tau_{n+1}^{j}(\beta)>\tau_{n}^{j}(\beta)$ for $0 \leq n<$ $N_{0}(\beta), j \in \mathbb{N}_{0}$.
2. If $k \leq 1$, then for any $\beta \in(0, k), \tau_{n+1}^{j}(\beta)>\tau_{n}^{j}(\beta)$ for $0 \leq n<N_{0}(\beta), j \in \mathbb{N}_{0}$.

Proof. If $k>1$, from (2.9),

$$
\begin{aligned}
\sigma_{n}^{2} & =\frac{-\left(A_{n}^{2}-2 B_{n}\right)+\sqrt{\left(A_{n}^{2}-2 B_{n}\right)^{2}-4\left(B_{n}^{2}-C^{2}\right)}}{2} \\
& =\frac{2}{\sqrt{\frac{\left(A_{n}^{2}-2 B_{n}\right)^{2}}{\left(C^{2}-B_{n}^{2}\right)^{2}}+\frac{4}{C^{2}-B_{n}^{2}}}+\frac{A_{n}^{2}-2 B_{n}}{C^{2}-B_{n}^{2}}},
\end{aligned}
$$

where $A_{n}^{2}-2 B_{n}$ and $B_{n}^{2}-C^{2}$ are given in (2.8). Since when $\beta \in[(k-1) / 2, k)$, $A_{n}^{2}-2 B_{n}$ is strictly increasing in $n$ and $C^{2}-B_{n}^{2}$ is strictly decreasing in $n$ for $0 \leq n<N_{0}(\beta)$, then we obtain $\sigma_{n+1}^{2}(\beta)<\sigma_{n}^{2}(\beta)$ when $\beta \in[(k-1) / 2, k)$. Since when $\beta \in[(k-1) / 2, k)$, then $A_{n} \geq 0$, and consequently from (2.11),

$$
\tau_{n}^{0}=\frac{\arccos \frac{\sigma_{n}^{2}-B_{n}}{C}}{\sigma_{n}}
$$

Hence we can obtain $\tau_{n+1}^{0}(\beta)>\tau_{n}^{0}(\beta), 0 \leq n<N_{0}(\beta)$.
Since $\sigma_{n+1}<\sigma_{n}$, then from (2.10) we can obtain that $\tau_{n+1}^{j}(\beta)>\tau_{n}^{j}(\beta), j \geq 1$, $0<n<N_{0}(\beta)$. Similarly we can obtain the second conclusion.

In the case of $k \leq 1$, then $A_{n}>0$ whenever $\beta \in \mathcal{D}_{n}$ and consequently from (2.11),

$$
\begin{equation*}
\tau_{n}^{j}(\beta)=\frac{\arccos \frac{\sigma_{n}^{2}-B_{n}}{C}+2 j \pi}{\sigma_{n}} \tag{2.13}
\end{equation*}
$$

Then we can arrive at the following results of curves $\tau_{n}^{j}(\beta)$ when $k \leq 1$.
Proposition 2.4. Suppose $d_{1}, d_{2}, k, r, l$ are all positive constants. Define $l_{n}=$ $\left(\frac{d_{1} d_{2} n^{4}}{r}\right)^{\frac{1}{4}}$, for $n \in \mathbb{N}_{0}$, then $\bigcup_{n=0}^{\infty}\left(l_{n}, l_{n+1}\right]=\mathbb{R}^{+}$. If $k \leq 1$, then for any $l \in$ $\left(l_{n}, l_{n+1}\right]$, there exist $\left\{\beta_{p}\right\}_{p=0}^{n}$ such that $\beta_{n}<\cdots<\beta_{p+1}<\beta_{p}<\cdots<\beta_{0}=k$ which satisfy the following properties:

1. $\mathcal{D}_{p}=\left(0, \beta_{p}\right)$ for $0 \leq p \leq n, \mathcal{D}_{p}=\emptyset$ for $p>n$, and $N=\max _{0<\beta<k} N_{0}(\beta)=n$;
2. $\tau_{p}^{j}(\beta)$ is a strictly increasing function for $\beta \in\left(0, \beta_{p}\right)$ where $0 \leq p \leq n$ and $j \in \mathbb{N}_{0}$;
3. For $j \in \mathbb{N}_{0}$ and $0 \leq p \leq n, \lim _{\beta \rightarrow \beta_{p}} \tau_{p}^{j}(\beta)=+\infty, \lim _{\beta \rightarrow 0} \tau_{p}^{0}(\beta)>0$ for $1 \leq p \leq n$, and $\lim _{\beta \rightarrow 0} \tau_{0}^{0}(\beta)=0$.
Proof. When $k \leq 1, B_{p}^{2}-C^{2}$ is strictly increasing in $\beta$ for $p \in \mathbb{N}_{0}$. Since for any $l \in$ $\left(l_{n}, l_{n+1}\right], \lim _{\beta \rightarrow 0}\left(B_{p}^{2}-C^{2}\right)<0$ for $0 \leq p \leq n$ and $\lim _{\beta \rightarrow 0}\left(B_{p}^{2}-C^{2}\right) \geq 0$ for $p>n$, then there exist $\left\{\beta_{p}\right\}_{p=0}^{n}$ such that $\beta_{n}<\cdots<\beta_{p+1}<\beta_{p}<\cdots<\beta_{0}=k$ satisfying $\mathcal{D}_{p}=\left(0, \beta_{p}\right)$ for $0 \leq p \leq n$ and $\mathcal{D}_{p}=\emptyset$ for $p>n$. So $N=\max _{0<\beta<k} N_{0}(\beta)=n$.

To prove that $\tau_{p}^{0}(\beta)$ is strictly increasing in $\beta$, we observe that

$$
\begin{aligned}
\sigma_{p}^{2} & =\frac{-\left(A_{p}^{2}-2 B_{p}\right)+\sqrt{\left(A_{p}^{2}-2 B_{p}\right)^{2}-4\left(B_{p}^{2}-C^{2}\right)}}{2} \\
& =\frac{2}{\sqrt{\frac{\left(A_{p}^{2}-2 B_{p}\right)^{2}}{\left(C^{2}-B_{p}^{2}\right)^{2}}+\frac{4}{C^{2}-B_{p}^{2}}}+\frac{A_{p}^{2}-2 B_{p}}{C^{2}-B_{p}^{2}}}
\end{aligned}
$$

and

$$
\begin{aligned}
\frac{\sigma_{p}^{2}}{C} & =\frac{-\left(A_{p}^{2}-2 B_{p}\right)+\sqrt{\left(A_{p}^{2}-2 B_{p}\right)^{2}-4\left(B_{p}^{2}-C^{2}\right)}}{2 C} \\
& =\frac{2}{\sqrt{\frac{\left(A_{p}^{2}-2 B_{p}\right)^{2} C^{2}}{\left(C^{2}-B_{p}^{2}\right)^{2}}+\frac{4 C^{2}}{C^{2}-B_{p}^{2}}}+\frac{C\left(A_{p}^{2}-2 B_{p}\right)}{C^{2}-B_{p}^{2}}} .
\end{aligned}
$$

Since $C^{2}-B_{p}^{2}$ is strictly decreasing in $\beta, \frac{C^{2}-B_{p}^{2}}{C}$ is strictly decreasing in $\beta, \frac{B_{p}}{C}$ is strictly increasing in $\beta$, and $A_{p}^{2}-2 B_{p}$ is strictly increasing in $\beta$, we can obtain that $\sigma_{p}$ and $\frac{\sigma_{p}^{2}}{C}$ are strictly decreasing in $\beta$. So from (2.13), $\tau_{p}^{j}(\beta)$ is a strictly increasing function when $\beta \in\left(0, \beta_{p}\right)$ for $0 \leq p \leq n, j \in \mathbb{N}_{0}$.

Since $\lim _{\beta \rightarrow \beta_{p}} \sigma_{p}(\beta)=0$ for $0 \leq p \leq n, \lim _{\beta \rightarrow 0} \sigma_{p}(\beta)>0$ for $1 \leq p \leq n$, and $\lim _{\beta \rightarrow 0} \arccos \frac{\sigma_{0}^{2}-B_{0}}{C}=0$, then from (2.13) we can obtain $\lim _{\beta \rightarrow \beta_{p}} \tau_{p}^{0}(\beta)=+\infty$ for $0 \leq p \leq n, \lim _{\beta \rightarrow 0} \tau_{p}^{0}(\beta)>0$ for $1 \leq p \leq n$ and $\lim _{\beta \rightarrow 0} \tau_{0}^{0}(\beta)=0$.

To visualize the curves $\tau_{n}^{j}(\beta)$ described in Proposition 2.4, we choose $d_{1}=$ $0.5, d_{2}=1, r=1, l=1$ and $k=1$, then in this case $l \in\left(l_{1}, l_{2}\right]$ and $N=2$. So from Proposition 2.4, there exist $\beta_{0}$ and $\beta_{1}$ as the asymptotes of $\tau_{0}^{j}(\beta)$ and $\tau_{1}^{j}(\beta)$, see Fig. 1.

In the case of $k>1$, the description of curves $\tau_{n}^{j}(\beta),\left(0 \leq n \leq N, j \in \mathbb{N}_{0}\right)$, is much more complicated. The difficulty is that in this case $\tau_{n}^{j}$ is defined piecewisely when $0<\beta<k$. When $\beta \geq(k-1) / 2$, we still have $A_{n} \geq 0$, so

$$
\tau_{n}^{j}(\beta)=\frac{\arccos \frac{\sigma_{n}^{2}-B_{n}}{C}+2 j \pi}{\sigma_{n}} .
$$

Then using the same method from Proposition 2.4 we first give the following description of $\tau_{n}^{j}(\beta)$ when $\beta \geq(k-1) / 2$.

Proposition 2.5. Suppose $d_{1}, d_{2}, k, l$ are all positive constant. Define $\tilde{l}_{n}=$ $\left(\frac{d_{1} d_{2} n^{4} k}{r}\right)^{\frac{1}{4}}, n \in \mathbb{N}_{0}$, then $\bigcup_{n=0}^{\infty}\left(\tilde{l}_{n}, \tilde{l}_{n+1}\right]=\mathbb{R}^{+}$. When $k>1$, for any $l \in\left(\tilde{l}_{n}, \tilde{l}_{n+1}\right]$, there exist $\left\{\tilde{\beta}_{p}\right\}_{p=0}^{n}$ such that $\tilde{\beta}_{n}<\cdots<\tilde{\beta}_{p+1}<\tilde{\beta}_{p}<\cdots<\tilde{\beta}_{0}=k$ satisfying:

1. $[(k-1) / 2, k) \bigcap \mathcal{D}_{p}=\left[(k-1) / 2, \tilde{\beta}_{p}\right)$ for $0 \leq p \leq n,[(k-1) / 2, k) \bigcap \mathcal{D}_{p}=\emptyset$ for $p>n$, and $N=\max _{0<\beta<k} N_{0}(\beta) \geq \max _{(k-1) / 2 \leq \beta<k} N_{0}(\beta)=n$;
2. $\tau_{p}^{j}(\beta)$ is a strictly increasing function for $\beta \in\left[(k-1) / 2, \tilde{\beta}_{p}\right), 0 \leq p \leq n$, $j \in \mathbb{N}_{0}$;
3. $\lim _{\beta \rightarrow \tilde{\beta}_{p}} \tau_{p}^{j}(\beta)=+\infty$ for $0 \leq p \leq n, j \in \mathbb{N}_{0}, \lim _{\beta \rightarrow(k-1) / 2} \tau_{P}^{0}(\beta)>0$, for $1 \leq p \leq n$, and $\lim _{\beta \rightarrow(k-1) / 2} \tau_{0}^{0}(\beta)=0$.


Figure 1. Graph of $\tau_{p}^{j}(\beta)$ when $k \leq 1$. Here $\beta_{0}=1, \beta_{1}=0.25$ and $p=0,1$, where we use $d_{1}=0.5, d_{2}=1, r=1, l=1$ and $k=1$. We only show the curves for $j=0,1$.

To visualize the curves $\tau_{n}^{j}(\beta)$ described in Proposition 2.5, we choose $d_{1}=$ $0.5, d_{2}=1, r=1, l=1$ and $k=1.5$, then in this case $l \in\left(\tilde{l}_{1}, \tilde{l}_{2}\right]$. So from Proposition 2.5, we obtain that there exist $\tilde{\beta}_{0}$ and $\tilde{\beta}_{1}$ as the asymptotes of $\tau_{0}^{j}(\beta)$ and $\tau_{1}^{j}(\beta)$, see Fig. 2.

Propositions 2.3, 2.4 and 2.5 show that when $k \leq 1$ or $k>1$ but $\beta>(k-1) / 2$, the curves of pure imaginary roots of Eq. $\left(2.5_{n}\right)$ have similar structure, and Lemma 2.2 guarantees the transversality condition for Hopf bifurcations at such points. Thus we have the following results:

Theorem 2.6. Suppose $d_{1}, d_{2}, k, l, r$ are all positive constants, and either $k>1$ and $(k-1) / 2 \leq \beta<k$, or $0<k \leq 1$ and $0<\beta<k$.
(i) if $\tau \in\left[0, \tau_{0}^{0}(\beta)\right)$, then all the roots of Eqs. $\left(2.5_{n}\right),(n \geq 0)$ have negative real parts, and the positive equilibrium $\left(\beta, v_{\beta}\right)$ is locally asymptotically stable.
(ii) if $\tau=\tau_{0}^{0}(\beta)$, then all the roots of Eq. $\left(2.5_{0}\right)$ except $\pm i \sigma_{0}$ and the ones of Eqs. $\left(2.5_{n}\right),(n \geq 1)$ have negative real parts, and system (2.1) undergoes a Hopf bifurcation at $\left(\beta, v_{\beta}\right)$.
(iii) if $\tau>\tau_{0}^{0}(\beta)$, the positive equilibrium $\left(\beta, v_{\beta}\right)$ is unstable with at least two roots of Eqs. $\left(2.5_{n}\right),(n \geq 0)$ with positive real parts. Moreover whenever $\tau$ increases through one of curves $\tau_{n}^{j}(\beta), 0 \leq n \leq N, j \in \mathbb{N}_{0}$, the sum of the multiplicities of the roots of Eqs. $\left(2.5_{n}\right)$ with positive real parts will increase by two.

Proof. When $k>1,(k-1) / 2<\beta<k$ or $k \leq 1,0<\beta<k$, then $\frac{\beta(k-1-2 \beta)}{k(1+\beta)}<0$. Hence it is easy to verify that all the roots of Eqs. $\left(2.5_{n}\right),(n \geq 0)$ have negative real parts when $\tau=0$. Hence, from the transversality condition in Lemma 2.2,


Figure 2. Graph of $\tau_{p}^{j}(\beta)$, when $k>1$. Here $\tilde{\beta}_{0}=1.5, \tilde{\beta}_{1}=0.375$, and $p=0,1$, where we use $d_{1}=0.5, d_{2}=1, r=1, l=1$ and $k=1.5$. We only show the curves for $j=0,1$.

Proposition 2.3-2.5 and the result of Ruan and Wei [18, Corollary 2.4], we can obtain the conclusion.

Remark 2.7. For a fixed $\beta$ as in Theorem 2.6, denote $\mathcal{P}(\beta)=\left\{\tau_{n}^{j}(\beta), 0 \leq n<\right.$ $N, j \in \mathbb{N}_{0}: \tau_{n}^{j} \neq \tau_{m}^{k}$, for any $\left.m \neq n, j \neq k\right\}$. then system (2.1) also undergoes a Hopf bifurcation at ( $\beta, v_{\beta}$ ) when $\tau \in \mathcal{P}(\beta)$.

To visualize the curves $\tau_{n}^{j}(\beta)$ in Theorem 2.6, we choose $k=1.5$ and plot $\tau_{p}^{j}, p=$ 0,1 for $0 \leq j \leq 9$ when $\beta>(k-1) / 2=0.25$ (see Fig. 3). From Fig. 3 we know that $\tau_{0}^{0}(\beta)$ is the lowest curve. So fixing $\beta$ and increasing $\tau$, we can see that $\left(\beta, v_{\beta}\right)$ loses its stability when $\tau$ pass through $\tau_{0}^{0}(\beta)$ and a Hopf bifurcation occurs at $\left(\beta, v_{\beta}\right)$ when $\tau$ passes through each bifurcation value in $\mathcal{P}(\beta)$. We can see when $\beta$ is close to 0.25 , the Hopf bifurcation value $\tau_{1}^{0}(\beta)$ belongs to $\mathcal{P}(\beta)$ and then system undergoes a Hopf bifurcation of spatially inhomogeneous periodic orbits at $\left(\beta, v_{\beta}\right)$ when $\tau=\tau_{1}^{0}(\beta)$.

Theorem 2.6 shows the effect of delay on the dynamics of predator-prey system (2.2). From [26], we know that when $0<k \leq 1$ or $k>1$ but $k-1 \leq \beta<k$, the constant positive equilibrium $\left(\beta, v_{\beta}\right)$ is globally asymptotically stable (when $(k-1) / 2 \leq \beta<k-1,\left(\beta, v_{\beta}\right)$ is locally asymptotically stable). However From Theorem 2.6 we can see that when $0<k \leq 1$ or $k>1$ but $(k-1) / 2 \leq \beta<k$, a large delay could destabilize the constant equilibrium.

For $k>1$ and $0<\beta \leq(k-1) / 2$, the constant equilibrium $\left(\beta, v_{\beta}\right)$ is unstable even when $\tau=0$. In [26], Yi, Wei and Shi studied the Hopf bifurcations and equilibrium bifurcations of system (2.2) when $\tau=0$ and using $\beta,(0<\beta \leq(k-1) / 2)$ as bifurcation parameter. In this parameter range, the curves $\tau_{n}^{j}(\beta)$ are not always defined, and they may have vertical asymptotes where the curves blow up to infinity.


Figure 3. Graph of $\tau_{p}^{j}(\beta)$ where $d_{1}=0.5, d_{2}=1, r=1, l=1$ and $k=1.5$. Here $p=0,1$. We only show the curves for $j=$ $0,1, \cdots, 9$.

But we point out that the values $\beta$ so that $\tau_{n}^{0}(\beta)=0$ are coincident to the Hopf bifurcation points found in [26], since when $\tau=0$, the characteristic equation $\lambda^{2}+A_{n} \lambda+B_{n}+C e^{-\lambda \tau}=0$ becomes $\lambda^{2}+A_{n} \lambda+B_{n}+C=0$, which is the same as the characteristic equation at $\left(\beta, v_{\beta}\right)$ without delay effect (see Eq. (2.39) of [26]). Hence the Hopf bifurcations described in [26] also exist for the system with delay effect (2.2). Similar to Theorem 2.6, this shows that the Hopf bifurcations are jointly driven by two parameters $\tau$ (delay) and $\beta$ (internal system parameter). We will not describe the Hopf bifurcations for this parameter range in details, but only state the following stability results from our discussions:

Proposition 2.8. Suppose $d_{1}, d_{2}, k, l, r$ are all positive constants, and $k, \beta$ satisfy $k>1$ and $0<\beta<(k-1) / 2$. Then for any $\tau \geq 0$, the positive equilibrium $\left(\beta, v_{\beta}\right)$ is unstable with at least two roots of Eqs. $\left(2.5_{n}\right),(n \geq 0)$ with positive real parts. Moreover whenever $\tau$ increases through one of curves $\tau_{n}^{j}(\beta), 0 \leq n \leq N, j \in \mathbb{N}_{0}$, the sum of the multiplicities of the roots of Eqs. $\left(2.5_{n}\right)$ with positive real parts will increase by two.

Proof. When $k>1,0<\beta<(k-1) / 2$, then $\frac{\beta(k-1-2 \beta)}{k(1+\beta)}>0$. It's easy to verify that Eqs. $\left(2.5_{n}\right),(n=0,1,2, \cdots)$ have at lest a pair of roots with positive real parts when $\tau=0$. Hence, from the transversality condition of Lemma 2.2 and the result of Ruan and Wei [18, Corollary 2.4], we derive the conclusion.

To conclude our discussion of the dynamics of (2.2), we show that when $0<m \leq$ $\frac{(1+k) r}{k}$, the dynamics is much simpler. Indeed when $0<m \leq \frac{(1+k) r}{k}$, system (2.1) has only two nonnegative equilibria $(0,0)$ and $(k, 0)$. It is easy to verify that $(0,0)$ is always unstable and $(k, 0)$ is locally asymptotically stable when $0<m \leq \frac{(1+k) r}{k}$.

Furthermore we can show that $(k, 0)$ is globally asymptotically stable with respect to all solutions with non-negative initial values.

Theorem 2.9. Suppose $d_{1}, d_{2}, l, k, m, r$ are all positive constants. When $0<$ $m<\frac{(1+k) r}{k}$, then the constant equilibrium $(k, 0)$ of (2.1) is globally asymptotically stable with respect to solutions with nonnegative initial value $\left(u_{0}(x, t), v_{0}(x, t)\right),(x, t)$ $\in \Omega \times[-\tau, 0]$ and $u(x, 0) \not \equiv 0, v(x, 0) \not \equiv 0$.

Proof. Let $(u(x, t), v(x, t))$ be a solution of system (2.1) with nonnegative initial value $\left(u_{0}(x, t), v_{0}(x, t)\right),(x, t) \in \Omega \times[-\tau, 0]$ and $u(x, 0) \not \equiv 0, v(x, 0) \not \equiv 0$. Since $0<m<\frac{(1+k) r}{k}$, we can choose $\epsilon_{0}$ such that $\frac{m(k+\epsilon)}{k+\epsilon+1}<r$ for any $\epsilon \in\left(0, \epsilon_{0}\right)$. Because

$$
\frac{\partial u}{\partial t}-d_{1} \Delta u=u\left(1-\frac{u}{k}\right)-\frac{m u v}{u+1} \leq u\left(1-\frac{u}{k}\right)
$$

then for any given sufficiently small $\epsilon$ satisfying $0<\epsilon<\min \left\{1 / m, \epsilon_{0}\right\}$, there exists $t_{0}\left(u_{0}, v_{0}\right)$ such that $u(x, t) \leq k+\epsilon$ and consequently,

$$
\frac{\partial v}{\partial t}-d_{2} \Delta v=-r v+\frac{m u(t-\tau) v}{u(t-\tau)+1} \leq v\left(-r+\frac{m(k+\epsilon)}{k+\epsilon+1}\right)
$$

for $t>t_{0}\left(u_{0}, v_{0}\right)+\tau$. Since $-r+\frac{m(k+\epsilon)}{k+\epsilon+1}<0$, then for the above given $\epsilon$, there exists $t_{1}\left(u_{0}, v_{0}\right)$ such that for any $t>t_{1}\left(u_{0}, v_{0}\right),\|v(x, t)\|_{C^{1}(\bar{\Omega})}<\epsilon$ and consequently,

$$
\frac{\partial u}{\partial t}-d_{1} \Delta u=u\left(1-\frac{u}{k}\right)-\frac{m u v}{u+1} \geq u\left(1-m \epsilon-\frac{u}{k}\right) .
$$

So $\lim _{t \rightarrow \infty} u(x, t)=k, \lim _{t \rightarrow \infty} v(x, t)=0$ in $C^{1}(\bar{\Omega})$.
3. Direction and stability of the Hopf bifurcation. In the previous section, we have already obtained that system (2.1) undergoes a Hopf bifurcation at ( $\beta, v_{\beta}$ ) when $\tau \in \mathcal{P}(\beta)$. In this section, we shall study the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions by employing the center manifold theorem due to Lin, So and Wu [13] and normal form method (see Wu [22], Hassard et al. [8]) for partial differential equations with delay. This procedure of computing normal form can also be carried out by the method of Faria (see $[4,5,2]$ ). Then we compute the direction and stability of the Hopf bifurcation when $\tau=\tau_{0} \equiv \tau_{0}^{0}(\beta) \in \mathcal{P}(\beta)$. The direction of the Hopf bifurcation when $\tau$ is equal to other Hopf bifurcation values in $\mathcal{P}(\beta)$ can also be analyzed using the same procedure.

Setting $\tau=\tau_{0}+\mu$, then $\mu=0$ is the Hopf bifurcation value of system (2.3). Re-scaling the time by $t \rightarrow \frac{t}{\tau}$ to normalize the delay, system (2.3) can be written in the form

$$
\begin{equation*}
\frac{d U(t)}{d t}=\tau_{0} d \Delta U(t)+\tau_{0} L_{0}\left(U_{t}\right)+G\left(U_{t}, \mu\right) \tag{3.1}
\end{equation*}
$$

where

$$
\begin{aligned}
& L_{0}(\phi)=\binom{\frac{\beta(k-1-2 \beta)}{k(1+\beta)} \phi_{1}(0)-r \phi_{2}(0)}{\frac{k-\beta}{k(\beta+1)} \phi_{1}(-1)} \\
& G(\phi, \mu)=\mu d \Delta \phi(0)+\mu L_{0}(\phi)+\left(\mu+\tau_{0}\right) F_{0}(\phi) \\
& F_{0}(\phi) \\
&=\binom{\frac{(k-\beta)}{k(1+\beta)} \phi_{1}(0)+r \phi_{2}(0)+\beta-\frac{\beta^{2}+\phi_{1}^{2}(0)}{k}-\frac{m\left(\phi_{1}(0)+\beta\right)\left(\phi_{2}(0)+v_{\beta}\right)}{\phi_{1}(0)+\beta+1}}{-\frac{(k-\beta)}{k(1+\beta)} \phi_{1}(-1)-r \phi_{2}(0)-r v_{\beta}+\frac{m\left(\phi_{1}(-1)+\beta\right)\left(\phi_{2}(0)+v_{\beta}\right)}{\phi_{1}(-1)+\beta+1}},
\end{aligned}
$$

for $\phi \in \mathcal{C}=C([-1,0], X)$.
From Section 2, we know that $\pm i \sigma_{0} \tau_{0}$ is a pair of simple purely imaginary eigenvalues of the linear system

$$
\begin{equation*}
\frac{d U(t)}{d t}=\tau_{0} d \Delta U(t)+\tau_{0} L_{0}\left(U_{t}\right) \tag{3.2}
\end{equation*}
$$

and the linear functional differential equation

$$
\begin{equation*}
\frac{d z(t)}{d t}=\tau_{0} L_{0}\left(z_{t}\right) \tag{3.3}
\end{equation*}
$$

By Riesz representation theorem, there exists a $2 \times 2$ matrix $\eta(\theta, \mu),(\theta \in[-1,0])$, whose elements are of bounded variation functions such that

$$
\begin{equation*}
\left(\tau_{0}+\mu\right) L_{0}(\phi)=\int_{-1}^{0} d \eta(\theta, \mu) \phi(\theta), \text { for } \phi(\theta) \in C\left([-1,0], \mathbb{R}^{2}\right) \tag{3.4}
\end{equation*}
$$

In fact, we have

$$
d \eta(\theta, \mu)=\left(\tau_{0}+\mu\right) E \delta(\theta)+\left(\tau_{0}+\mu\right) F \delta(\theta+1)
$$

where

$$
E=\left(\begin{array}{cc}
\frac{\beta(k-1-2 \beta)}{k(1+\beta)} & -r \\
0 & 0
\end{array}\right), \quad F=\left(\begin{array}{cc}
0 & 0 \\
\frac{k-\beta}{k(1+\beta)} & 0
\end{array}\right)
$$

Then (3.4) is satisfied.
For $\phi(\theta) \in C^{1}\left([-1,0], \mathbb{R}^{2}\right)$, define $A(0)$ as

$$
A(0)(\phi(\theta))= \begin{cases}\frac{d \phi(\theta)}{d \theta}, & \theta \in[-1,0) \\ \int_{-1}^{0} d \eta(\theta, 0) \phi(\theta), & \theta=0\end{cases}
$$

and for $\psi=\left(\psi_{1}, \psi_{2}\right) \in C^{1}\left([0,1],\left(\mathbb{R}^{2}\right)^{*}\right)$, define

$$
A^{*}(\psi(s))= \begin{cases}-\frac{d \psi(s)}{d s}, & s \in(0,1] \\ \int_{-1}^{0} \psi(-\xi) d \eta(\theta, 0), & s=0\end{cases}
$$

Then $A(0)$ and $A^{*}$ are adjoint operators under the bilinear form

$$
(\psi(s), \phi(\theta))_{0}=\bar{\psi}(0) \phi(0)-\int_{-1}^{0} \int_{0}^{\theta} \bar{\psi}(\xi-\theta) d \eta(0, \theta) \phi(\xi) d \xi
$$

where $\psi(s) \in C\left([0,1],\left(\mathbb{R}^{2}\right)^{*}\right)$ and $\phi(\theta) \in C\left([-1,0], \mathbb{R}^{2}\right)$ (see Hale [7, Chapter 7], Hassard et.al. [8]).

It can be verified that $\pm i \sigma_{0} \tau_{0}$ are the eigenvalues of $A(0)$ and $A^{*}$, and $q(\theta)=$ $\left(q_{1}, q_{2}\right)^{T} e^{i \sigma_{0} \tau_{0} \theta}(\theta \in[-1,0])$ and $q^{*}(s)=\frac{1}{D}\left(q_{1}^{*}, q_{2}^{*}\right) e^{i \sigma_{0} \tau_{0} s}(s \in[0,1])$ are the eigenvectors of $A(0)$ and $A^{*}$ corresponding to the eigenvalue $i \sigma_{0} \tau_{0}$ and $-i \sigma_{0} \tau_{0}$, respectively, where

$$
\begin{aligned}
& \left(q_{1}, q_{2}\right)=\left(1, \frac{\beta(k-1-2 \beta)}{r k(1+\beta)}-\frac{i \sigma_{0}}{r}\right),\left(q_{1}^{*}, q_{2}^{*}\right)=\left(1,-\frac{i r}{\sigma_{0}}\right), \\
& D=2+\frac{i \beta(k-1-2 \beta)}{\sigma_{0} k(1+\beta)}+\frac{i r(k-\beta) \tau_{0} e^{-i \sigma_{0} \tau_{0}}}{\sigma_{0} k(1+\beta)}
\end{aligned}
$$

Let $\Phi=(q(\theta), \bar{q}(\theta)), \Psi=\left(q^{*}(s), \bar{q}^{*}(s)\right)^{T}$, then $(\Psi, \Phi)_{0}=I$, where $I=\left(\begin{array}{ll}1 & 0 \\ 0 & 1\end{array}\right)$. Then the center subspace of system (3.3) is $P=\operatorname{span}\{q(\theta), \bar{q}(\theta)\}$, and the adjoint subspace is $P^{*}=\operatorname{span}\left\{q^{*}(s), \bar{q}^{*}(s)\right\}$.

Let $f_{0}=\left(f_{0}^{1}, f_{0}^{2}\right)^{T}$, where

$$
f_{0}^{1}=\binom{1}{0}, f_{0}^{2}=\binom{0}{1}
$$

By using the notation from Wu [22], we also define $c \cdot f_{0}=c_{1} f_{0}^{1}+c_{2} f_{0}^{2}$ for $c=$ $\left(c_{1}, c_{2}\right)^{T} \in \mathbb{C}^{2},\left(\psi \cdot f_{0}\right)(\theta)=\psi(\theta) \cdot f_{0}$ for $\psi(\theta) \in[-1,0]$ and

$$
\langle u, v\rangle=\frac{1}{l \pi} \int_{0}^{l \pi} u_{1} \bar{v}_{1} d x+\frac{1}{l \pi} \int_{0}^{l \pi} u_{2} \bar{v}_{2} d x
$$

for $u=\left(u_{1}, u_{2}\right), v=\left(v_{1}, v_{2}\right) \in X=C\left([0, l \pi], \mathbb{R}^{2}\right)$. Hence $\left\langle\phi, f_{0}\right\rangle=\left(\left\langle\phi, f_{0}^{1}\right\rangle,\left\langle\phi, f_{0}^{2}\right\rangle\right)^{T}$ where $\phi \in \mathcal{C}=C([-1,0], X)$.

Then the center subspace of linear system (3.2) is given by $P_{C N} \mathcal{C}$, where

$$
\begin{aligned}
& P_{C N} \phi=\Phi\left(\Psi,\left\langle\phi, f_{0}\right\rangle\right)_{0} \cdot f_{0}, \phi \in \mathcal{C}, \\
& P_{C N} \mathcal{C}=\left\{(q(\theta) z+\bar{q}(\theta) \bar{z}) \cdot f_{0}: z \in \mathbb{C}\right\},
\end{aligned}
$$

and $\mathcal{C}=P_{C N} \mathcal{C} \oplus P_{S} \mathcal{C}$, where $P_{s} \mathcal{C}$ is the stable subspace.
From Wu [22], we know that the infinitesimal generator $A_{U}$ of linear system (3.2) satisfies

$$
A_{U} \psi=\dot{\psi}(\theta)
$$

Moreover $\psi \in \operatorname{dom}\left(A_{U}\right)$ if and only if

$$
\dot{\psi}(\theta) \in \mathcal{C}, \psi(0) \in \operatorname{dom}(\triangle), \dot{\psi}(\theta)(0)=\tau_{0} \Delta \psi(0)+\tau_{0} L_{0}(\psi)
$$

As the formulas to be developed for the bifurcation direction and stability are all relative to $\mu=0$ only, we set $\mu=0$ in system (3.1) and obtain a center manifold

$$
\begin{equation*}
W(z, \bar{z})=W_{20}(\theta) \frac{z^{2}}{2}+W_{11}(\theta) z \bar{z}+W_{02}(\theta) \frac{\bar{z}^{2}}{2}+\cdots \tag{3.5}
\end{equation*}
$$

with the range in $P_{S} \mathcal{C}$. The flow of system (3.1) in the center manifold can be written as follows:

$$
u_{t}=\Phi(z(t), \bar{z}(t))^{T} \cdot f_{0}+W(z(t), \bar{z}(t)),
$$

where

$$
\begin{equation*}
\dot{z}(t)=i \sigma_{0} \tau_{0} z(t)+\overline{q^{*}(0)}\left\langle G\left(\Phi(z(t), \bar{z}(t))^{T} \cdot f_{0}+W(z, \bar{z}), 0\right), f_{0}\right\rangle . \tag{3.6}
\end{equation*}
$$

We rewrite (3.6) as

$$
\begin{equation*}
\dot{z}(t)=i \sigma_{0} \tau_{0} z(t)+g(z, \bar{z}) \tag{3.7}
\end{equation*}
$$

with

$$
\begin{align*}
g(z, \bar{z}) & =\overline{q^{*}(0)}\left\langle G\left(\Phi(z(t), \bar{z}(t))^{T} \cdot f_{0}+W(z, \bar{z}), 0\right), f_{0}\right\rangle \\
& =g_{20} \frac{z^{2}}{2}+g_{11} z \bar{z}+g_{02} \frac{\bar{z}^{2}}{2}+g_{21} \frac{z^{2} \bar{z}}{2}+\cdots . \tag{3.8}
\end{align*}
$$

Denote

$$
f(u, v)=\frac{m(u+\beta)\left(v+v_{\beta}\right)}{u+\beta+1}
$$

and then from Taylor formula we have

$$
\begin{align*}
f(u, v)= & \beta-\frac{\beta^{2}}{k}+\frac{(k-\beta) u}{k(1+\beta)}+r v-\frac{(k-\beta) u^{2}}{k(1+\beta)^{2}} \\
& +\frac{m u v}{(\beta+1)^{2}}+\frac{(k-\beta) u^{3}}{k(1+\beta)^{3}}-\frac{m u^{2} v}{(\beta+1)^{3}}+O(4) \tag{3.9}
\end{align*}
$$

where $O(4)=O\left(\|(u, v)\|^{4}\right)$, and $G(\phi, 0)=\tau_{0}\left(G_{1}, G_{2}\right)^{T}$, where

$$
\begin{align*}
G_{1}= & \left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) \phi_{1}^{2}(0)-\frac{m}{(\beta+1)^{2}} \phi_{1}(0) \phi_{2}(0) \\
& -\frac{k-\beta}{k(1+\beta)^{3}} \phi_{1}^{3}(0)+\frac{m}{(\beta+1)^{3}} \phi_{1}^{2}(0) \phi_{2}(0)+O(4) \\
G_{2}= & -\frac{k-\beta}{k(1+\beta)^{2}} \phi_{1}^{2}(-1)+\frac{m}{(\beta+1)^{2}} \phi_{1}(-1) \phi_{2}(0)  \tag{3.10}\\
& +\frac{k-\beta}{k(1+\beta)^{3}} \phi_{1}^{3}(-1)-\frac{m}{(\beta+1)^{3}} \phi_{1}^{2}(-1) \phi_{2}(0)+O(4)
\end{align*}
$$

From (3.8) and (3.10), we have

$$
\begin{aligned}
g_{20}= & \frac{2 \bar{q}_{1}^{*} \tau_{0}}{D}\left[\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1}^{2}-\frac{m}{(1+\beta)^{2}} q_{1} q_{2}\right] \\
& +\frac{2 \bar{q}_{2}^{*} \tau_{0}}{D}\left[-\frac{k-\beta}{k(1+\beta)^{2}} q_{1}^{2} e^{-2 i \sigma_{0} \tau_{0}}+\frac{m}{(1+\beta)^{2}} q_{1} q_{2} e^{-i \sigma_{0} \tau_{0}}\right] \\
g_{11}= & \frac{\bar{q}_{1}^{*} \tau_{0}}{D}\left[2\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1} \bar{q}_{1}-\frac{m}{(1+\beta)^{2}}\left(q_{1} \bar{q}_{2}+\bar{q}_{1} q_{2}\right)\right] \\
& +\frac{\bar{q}_{2}^{*} \tau_{0}}{D}\left[-2 \frac{k-\beta}{k(1+\beta)^{2}} q_{1} \bar{q}_{1}+\frac{m}{(1+\beta)^{2}}\left(q_{1} \bar{q}_{2} e^{-i \sigma_{0} \tau_{0}}+\bar{q}_{1} q_{2} e^{i \sigma_{0} \tau_{0}}\right)\right] \\
g_{02}= & \frac{2 \bar{q}_{1}^{*} \tau_{0}}{D}\left[\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) \bar{q}_{1}^{2}-\frac{m}{(1+\beta)^{2}} \bar{q}_{1} \bar{q}_{2}\right] \\
& +\frac{2 \bar{q}_{2}^{*} \tau_{0}}{D}\left[-\frac{k-\beta}{k(1+\beta)^{2}} \bar{q}_{1}^{2} e^{2 i \sigma_{0} \tau_{0}}+\frac{m}{(1+\beta)^{2}} \bar{q}_{1} \bar{q}_{2} e^{i \sigma_{0} \tau_{0}}\right]
\end{aligned}
$$

$$
\begin{aligned}
g_{21}= & \frac{2 \bar{q}_{1}^{*} \tau_{0}}{D}\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) \frac{1}{l \pi} \int_{0}^{l \pi}\left(W_{20}^{1}(0) \bar{q}_{1}+2 W_{11}^{1}(0) q_{1}\right) d x \\
& -\frac{2 \bar{q}_{2}^{*} \tau_{0}}{D} \frac{k-\beta}{k(1+\beta)^{2}} \frac{1}{l \pi} \int_{0}^{l \pi}\left(2 e^{-i \sigma_{0} \tau_{0}} W_{11}^{1}(-1) q_{1}+e^{i \sigma_{0} \tau_{0}} W_{20}^{1}(-1) \bar{q}_{1}\right) d x \\
& -\frac{\bar{q}_{1}^{*} \tau_{0} m}{D(1+\beta)^{2}} \frac{1}{l \pi} \int_{0}^{l \pi}\left(W_{20}^{1}(0) \bar{q}_{2}+2 W_{11}^{1}(0) q_{2}\right) d x \\
& -\frac{\bar{q}_{1}^{*} \tau_{0} m}{D(1+\beta)^{2}} \frac{1}{l \pi} \int_{0}^{l \pi}\left(+W_{20}^{2}(0) \bar{q}_{1}+2 W_{11}^{2}(0) q_{1}\right) d x \\
& +\frac{\bar{q}_{2}^{*} \tau_{0} m}{D(1+\beta)^{2}} \frac{1}{l \pi} \int_{0}^{l \pi}\left(W_{20}^{1}(-1) \bar{q}_{2}+2 W_{11}^{1}(-1) q_{2}\right) d x \\
& +\frac{\bar{q}_{2}^{*} \tau_{0} m}{D(1+\beta)^{2}} \frac{1}{l \pi} \int_{0}^{l \pi}\left(W_{20}^{2}(0) \bar{q}_{1} e^{i \sigma_{0} \tau_{0}}+2 W_{11}^{2}(0) q_{1} e^{-i \sigma_{0} \tau_{0}}\right) d x \\
& +\frac{2 \tau_{0} m}{D(1+\beta)^{3}}\left(\bar{q}_{1}^{*} q_{1}^{2} \bar{q}_{2}+2 \bar{q}_{1}^{*} q_{1} q_{2} \bar{q}_{1}-\bar{q}_{2}^{*} q_{1}^{2} \bar{q}_{2} e^{-2 i \sigma_{0} \tau_{0}}-2 \bar{q}_{2}^{*} q_{1} q_{2} \bar{q}_{1}\right) \\
& +\frac{2(k-\beta) \tau_{0}}{D k(1+\beta)^{3}}\left(3 \bar{q}_{2}^{*} q_{1}^{2} \bar{q}_{1} e^{-i \sigma_{0} \tau_{0}}-3 \bar{q}_{1}^{*} q_{1}^{2} \bar{q}_{1}\right) .
\end{aligned}
$$

So in order to compute $g_{21}$, we need to compute $W_{20}(\theta)$ and $W_{11}(\theta)$.
Since $W(z(t),(z(t))$ satisfies

$$
\begin{align*}
\dot{W}= & A_{U} W+X_{0} G\left(\Phi(z, \bar{z})^{T} \cdot f_{0}+w(z, \bar{z}), 0\right) \\
& -\Phi\left(\Psi,\left\langle X_{0} G\left(\Phi(z, \bar{z})^{T} \cdot f_{0}+w(z, \bar{z}), 0\right), f_{0}\right\rangle\right)_{0} \cdot f_{0}  \tag{3.11}\\
= & A_{U} W+H_{20} \frac{z^{2}}{2}+H_{11} z \bar{z}+H_{02} \frac{\bar{z}^{2}}{2}+\cdots,
\end{align*}
$$

then by using the chain rule

$$
\dot{W}=\frac{\partial W(z, \bar{z})}{\partial z} \dot{z}+\frac{\partial W(z, \bar{z})}{\partial \bar{z}} \dot{\bar{z}}
$$

we have that

$$
\left\{\begin{array}{l}
{\left[2 i \sigma_{0} \tau_{0}-A_{U}\right] W_{20}=H_{20}}  \tag{3.12}\\
-A_{U} W_{11}=H_{11} \\
{\left[-2 i \sigma_{0} \tau_{0}-A_{U}\right] W_{02}=H_{02}}
\end{array}\right.
$$

Note that for $-1 \leq \theta<0$,
$-\Phi\left(\Psi,\left\langle X_{0} G\left(\Phi(z, \bar{z})^{T} \cdot f_{0}+w(z, \bar{z}), 0\right), f_{0}\right\rangle\right)_{0} \cdot f_{0}=H_{20} \frac{z^{2}}{2}+H_{11} z \bar{z}+H_{02} \frac{\bar{z}^{2}}{2}+\cdots$,
then we have for $-1 \leq \theta<0$,

$$
\begin{align*}
& H_{20}(\theta)=-\left[g_{20} q(\theta)+\bar{g}_{02} \bar{q}(\theta)\right] \cdot f_{0}  \tag{3.13}\\
& H_{11}(\theta)=-\left[g_{11} q(\theta)+\bar{g}_{11} \bar{q}(\theta)\right] \cdot f_{0} \tag{3.14}
\end{align*}
$$

therefore from (3.12)

$$
W_{20}(\theta)=\frac{i g_{20}}{\sigma_{0} \tau_{0}} q(\theta) \cdot f_{0}+\frac{i \bar{g}_{02}}{3 \sigma_{0} \tau_{0}} \bar{q}(\theta) \cdot f_{0}+E_{1} e^{2 i \sigma_{0} \tau_{0} \theta}
$$

and

$$
W_{11}(\theta)=-\frac{i g_{11}}{\sigma_{0} \tau_{0}} q(\theta) \cdot f_{0}+\frac{i \bar{g}_{11}}{\sigma_{0} \tau_{0}} \bar{q}(\theta) \cdot f_{0}+E_{2}
$$

From (3.12) with $\theta=0$, the definition of $A_{U}$ and

$$
H_{20}(0)=-\left[g_{20} q(0)+\bar{g}_{02} \bar{q}(0)\right] \cdot f_{0}+\tau_{0}\binom{\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1}^{2}-\frac{m}{(1+\beta)^{2}} q_{1} q_{2}}{-\frac{k-\beta}{k(1+\beta)^{2}} q_{1}^{2} e^{-2 i \sigma_{0} \tau_{0}}+\frac{m}{(1+\beta)^{2}} q_{1} q_{2} e^{-i \sigma_{0} \tau_{0}}}
$$

we obtain

$$
\begin{equation*}
E_{1}=E_{11} \cdot E_{12}, \quad \text { and } \quad E_{2}=E_{21} \cdot E_{22} \tag{3.15}
\end{equation*}
$$

where

$$
\begin{aligned}
& E_{11}=\left(\begin{array}{cc}
2 i \sigma_{0}-\frac{\beta(k-1-2 \beta)}{k(1+\beta)} & r \\
-\frac{k-\beta}{k(1+\beta)} e^{-2 i \sigma_{0} \tau_{0}} & 2 i \sigma_{0}
\end{array}\right)^{-1} \\
& E_{12}=\binom{\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1}^{2}-\frac{m}{(1+\beta)^{2}} q_{1} q_{2}}{-\frac{k-\beta}{k(1+\beta)^{2}} q_{1}^{2} e^{-2 i \sigma_{0} \tau_{0}}+\frac{m}{(1+\beta)^{2}} q_{1} q_{2} e^{-i \sigma_{0} \tau_{0}}}
\end{aligned}
$$

and

$$
\begin{aligned}
& E_{21}=\left(\begin{array}{cc}
-\frac{\beta(k-1-2 \beta)}{k(1+\beta)} & r \\
-\frac{k-\beta}{k(1+\beta)} & 0
\end{array}\right)^{-1}, \\
& E_{22}=\binom{2\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1} \bar{q}_{1}-\frac{m}{(1+\beta)^{2}}\left(q_{1} \bar{q}_{2}+\bar{q}_{1} q_{2}\right)}{-2 \frac{k-\beta}{k(1+\beta)^{2}} q_{1} \bar{q}_{1}+\frac{m}{(1+\beta)^{2}}\left(q_{1} \bar{q}_{2} e^{-i \sigma_{0} \tau_{0}}+\bar{q}_{1} q_{2} e^{i \sigma_{0} \tau_{0}}\right)}
\end{aligned}
$$

Then $g_{21}$ can be determined.
Based on the above analysis, we can see that each $g_{i j}$ can be determined by the parameters. Thus we can compute the following quantities which determine the direction and stability of bifurcating periodic orbits:

$$
\begin{aligned}
& C_{1}(0)=\frac{i}{2 \sigma_{0} \tau_{0}^{0}}\left(g_{11} g_{20}-2\left|g_{11}\right|^{2}-\frac{\left|g_{02}\right|^{2}}{3}\right)+\frac{g_{21}}{2}, \quad \mu_{2}=-\frac{\operatorname{Re}\left(C_{1}(0)\right)}{\operatorname{Re}\left(\lambda^{\prime}\left(\tau_{0}^{0}\right)\right)} \\
& \beta_{2}=2 \operatorname{Re}\left(C_{1}(0)\right), \quad T_{2}=-\frac{\operatorname{Im}\left(C_{1}(0)\right)+\mu_{2} \operatorname{Im}\left(\lambda^{\prime}\left(\tau_{0}^{0}\right)\right)}{\sigma_{0} \tau_{0}^{0}}
\end{aligned}
$$

Theorem 3.1. For system (2.1),
(i) $\mu_{2}$ determines the direction of the Hopf bifurcation: if $\mu_{2}>0\left(\mu_{2}<0\right)$, then the bifurcating periodic solutions exist for $\tau>\tau_{0}=\tau_{0}^{0}\left(\tau<\tau_{0}=\tau_{0}^{0}\right)$;
(ii) $\beta_{2}$ determines the stability of bifurcating periodic solutions: the bifurcating periodic solutions are orbitally asymptotically stable (unstable) if $\beta_{2}<0\left(\beta_{2}>\right.$ 0);
(iii) $T_{2}$ determines the period of the bifurcating periodic solutions: the period increases (decreases) if $T_{2}>0\left(T_{2}<0\right)$.

A general conclusion regarding the direction and stability of bifurcating periodic orbits cannot be stated due to the complicated nature of computation. But for given parameter values, a calculation can be carried out by using the formulas
above. In the following, we present some numerical simulations to illustrate the analytic results.


Figure 4. The solution of system (2.1) tends to the positive equilibrium $(1,1 / 3)$. Here $\tau=2.1$ and the initial values: $u(x, t)=$ $1+0.01 t \cos x, v(x, t)=1 / 3+0.01 t \sin x, t \in[-2.1,0], x \in[0, \pi]$.


Figure 5. The solution of system (2.1) tends to a periodic orbit. Here $\tau=3.7$ and the initial values: $u(x, t)=1+$ $0.01 t \cos x, v(x, t)=1 / 3+0.01\left(x^{2}+t\right), t \in[-3.7,0], x \in[0, \pi]$.

We use a set of parameters as in Section 2:

$$
d_{1}=0.5, d_{2}=1, k=1.5, l=1
$$

and we also choose $m=2, r=1$. In this case $\beta=1$, and we examine the effect of delay on the dynamics of the system (2.1). We can compute that $\tau_{0}^{0}=3.6276$, $\sigma_{0}=0.2887$, and $\operatorname{Re}\left(C_{1}(0)\right)<0$. From Theorem 2.6 and Theorem 3.1 we obtain that for $\tau \in(0,3.6276)$, the positive equilibrium $(1,1 / 3)$ is stable. When $\tau$ is in a small right-side neighborhood of 3.6276 , system (2.1) has stable periodic solutions which bifurcate from the constant equilibrium $(1,1 / 3)$. The results are illustrated in Fig. 4 and Fig. 5 in which the left panel shows the graph of $u(x, t)$ and the right panel shows the one of $v(x, t)$.

Finally we indicate that how the procedure described in this section can be modified for the Hopf bifurcation in more general situation when $\tau=\tau_{n}^{j} \in \mathcal{P}(\beta)$.

We replace $\tau_{0}$ and $\sigma_{0}$ in the calculation above by $\tau_{n}^{j}$ and $\sigma_{n}$ respectively. Then in this case,

$$
E=\left(\begin{array}{cc}
\frac{\beta(k-1-2 \beta)}{k(1+\beta)}-\frac{d_{1} n^{2}}{l^{2}} & -r \\
0 & -\frac{d_{2} n^{2}}{l^{2}}
\end{array}\right), \quad F=\left(\begin{array}{cc}
0 & 0 \\
\frac{k-\beta}{k(1+\beta)} & 0
\end{array}\right)
$$

and

$$
\begin{aligned}
& \left(q_{1}, q_{2}\right)=\left(1, \frac{\beta(k-1-2 \beta)}{r k(1+\beta)}-\frac{i \sigma_{n}}{r}-\frac{d_{1} n^{2}}{r l^{2}}\right), \quad\left(q_{1}^{*}, q_{2}^{*}\right)=\left(1, \frac{-r}{\frac{q_{2} d_{2} n^{2}}{l^{2}}-i \sigma_{n}}\right) \\
& D=q_{1} \overline{q_{1}^{*}}+q_{2} \overline{q_{2}^{*}}+\frac{q_{1} \overline{q_{2}^{*}} \tau_{0} e^{-i \sigma_{n} \tau_{n}^{j}}(k-\beta)}{k(1+\beta)}
\end{aligned}
$$

Also in this case, denote

$$
f_{0}^{1}=\binom{\gamma_{n}}{0}, f_{0}^{2}=\binom{0}{\gamma_{n}}
$$

where $\gamma_{n}=\sqrt{2} \cos \frac{n x}{l}$, and for $u=\left(u_{1}, u_{2}\right), v=\left(v_{1}, v_{2}\right) \in X=C\left([0, l \pi], \mathbb{R}^{2}\right)$, define

$$
\langle u, v\rangle=\left\langle u_{1}, v_{1}\right\rangle_{0}+\left\langle u_{2}, v_{2}\right\rangle_{0}
$$

where

$$
\langle s, h\rangle_{0}=\frac{1}{l \pi} \int_{0}^{l \pi} \operatorname{shdx}
$$

for $s, h \in C([0, l \pi], \mathbb{R})$. Hence we can compute $g_{20}, g_{11}, g_{02}$ and $g_{21}$ as follows:

$$
\begin{aligned}
g_{20}= & \frac{2 \bar{q}_{1}^{*} \tau_{0}}{D}\left[\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1}^{2}-\frac{m}{(1+\beta)^{2}} q_{1} q_{2}\right]\left\langle\gamma_{n}^{2}, \gamma_{n}\right\rangle_{0} \\
& +\frac{2 \bar{q}_{2}^{*} \tau_{0}}{D}\left[-\frac{k-\beta}{k(1+\beta)^{2}} q_{1}^{2} e^{-2 i \sigma_{n} \tau_{n}^{j}}+\frac{m}{(1+\beta)^{2}} q_{1} q_{2} e^{-i \sigma_{n} \tau_{n}^{j}}\right]\left\langle\gamma_{n}^{2}, \gamma_{n}\right\rangle_{0}, \\
g_{11}= & \frac{\bar{q}_{1}^{*} \tau_{0}}{D}\left[2\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1} \bar{q}_{1}-\frac{m}{(1+\beta)^{2}}\left(q_{1} \bar{q}_{2}+\bar{q}_{1} q_{2}\right)\right]\left\langle\gamma_{n}^{2}, \gamma_{n}\right\rangle_{0} \\
& +\frac{\bar{q}_{2}^{*} \tau_{0}}{D}\left[-2 \frac{k-\beta}{k(1+\beta)^{2}} q_{1} \bar{q}_{1}+\frac{m}{(1+\beta)^{2}}\left(q_{1} \bar{q}_{2} e^{-i \sigma_{n} \tau_{n}^{j}}+\bar{q}_{1} q_{2} e^{i \sigma_{n} \tau_{n}^{j}}\right)\right]\left\langle\gamma_{n}^{2}, \gamma_{n}\right\rangle_{0}, \\
g_{02}= & \frac{2 \bar{q}_{1}^{*} \tau_{0}}{D}\left[\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) \bar{q}_{1}^{2}-\frac{m}{(1+\beta)^{2}} \bar{q}_{1} \bar{q}_{2}\right]\left\langle\gamma_{n}^{2}, \gamma_{n}\right\rangle_{0} \\
& +\frac{2 \bar{q}_{2}^{*} \tau_{0}}{D}\left[-\frac{k-\beta}{k(1+\beta)^{2}} \bar{q}_{1}^{2} e^{2 i \sigma_{n} \tau_{n}^{j}}+\frac{m}{(1+\beta)^{2}} \bar{q}_{1} \bar{q}_{2} e^{i \sigma_{n} \tau_{n}^{j}}\right]\left\langle\gamma_{n}^{2}, \gamma_{n}\right\rangle_{0},
\end{aligned}
$$

$$
\begin{aligned}
g_{21}= & \frac{2 \bar{q}_{1}^{*} \tau_{0}}{D}\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right)\left(\bar{q}_{1}\left\langle W_{20}^{1}(0) \gamma_{n}, \gamma_{n}\right\rangle_{0}+2 q_{1}\left\langle W_{11}^{1}(0) \gamma_{n}, \gamma_{n}\right\rangle_{0}\right) \\
& -\frac{2 \bar{q}_{2}^{*} \tau_{0}}{D} \frac{k-\beta}{k(1+\beta)^{2}}\left(2 e^{-i \sigma_{n} \tau_{n}^{j}} q_{1}\left\langle W_{11}^{1}(-1) \gamma_{n}, \gamma_{n}\right\rangle_{0}\right) \\
& -\frac{2 \bar{q}_{2}^{*} \tau_{0}}{D} \frac{k-\beta}{k(1+\beta)^{2}}\left(e^{i \sigma_{n} \tau_{n}^{j}} \bar{q}_{1}\left\langle W_{20}^{1}(-1) \gamma_{n}, \gamma_{n}\right\rangle_{0}\right) \\
& -\frac{\bar{q}_{1}^{*} \tau_{0} m}{D(1+\beta)^{2}}\left(\left\langle W_{20}^{1}(0) \gamma_{n}, \gamma_{n}\right\rangle_{0} \bar{q}_{2}+2\left\langle W_{11}^{1}(0) \gamma_{n}, \gamma_{n}\right\rangle_{0} q_{2}\right) \\
& -\frac{\bar{q}_{1}^{*} \tau_{0} m}{D(1+\beta)^{2}}\left(\left\langle W_{20}^{2}(0) \gamma_{n}, \gamma_{n}\right\rangle_{0} \bar{q}_{1}+2\left\langle W_{11}^{2}(0) \gamma_{n}, \gamma_{n}\right\rangle_{0} q_{1}\right) \\
& +\frac{\bar{q}_{2}^{*} \tau_{0} m}{D(1+\beta)^{2}}\left(\left\langle W_{20}^{1}(-1) \gamma_{n}, \gamma_{n}\right\rangle_{0} \bar{q}_{2}+2\left\langle W_{11}^{1}(-1) \gamma_{n}, \gamma_{n}\right\rangle_{0} q_{2}\right) \\
& +\frac{\bar{q}_{2}^{*} \tau_{0} m}{D(1+\beta)^{2}}\left(\left\langle W_{20}^{2}(0) \gamma_{n}, \gamma_{n}\right\rangle_{0} \bar{q}_{1} e^{i \sigma_{n} \tau_{n}^{j}}+2\left\langle W_{11}^{2}(0) \gamma_{n}, \gamma_{n}\right\rangle_{0} q_{1} e^{-i \sigma_{n} \tau_{n}^{j}}\right) \\
& +\frac{2 \tau_{0} m}{D(1+\beta)^{3}}\left(\bar{q}_{1}^{*} q_{1}^{2} \bar{q}_{2}+2 \bar{q}_{1}^{*} q_{1} q_{2} \bar{q}_{1}-\bar{q}_{2}^{*} q_{1}^{2} \bar{q}_{2} e^{-2 i \sigma_{n} \tau_{n}^{j}}-2 \bar{q}_{2}^{*} q_{1} q_{2} \bar{q}_{1}\right)\left\langle\gamma_{n}^{3}, \gamma_{n}\right\rangle_{0} \\
& +\frac{2(k-\beta) \tau_{0}}{D k(1+\beta)^{3}}\left(3 \bar{q}_{2}^{*} q_{1}^{2} \bar{q}_{1} e^{-i \sigma_{n} \tau_{n}^{j}}-3 \bar{q}_{1}^{*} q_{1}^{2} \bar{q}_{1}\right)\left\langle\gamma_{n}^{3}, \gamma_{n}\right\rangle_{0} .
\end{aligned}
$$

Since $2 \sigma_{n}$ is not the eigenvalue of characteristic equation (2.5), then $E_{1}$ can be uniquely determined by

$$
\begin{aligned}
& 2 i \sigma_{n} E_{1}-d \Delta E_{1}-L\left(e^{2 i \sigma_{n} \cdot} E_{1}\right) \\
= & \binom{\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1}^{2}-\frac{m}{(1+\beta)^{2}} q_{1} q_{2}}{-\frac{k-\beta}{k(1+\beta)^{2}} q_{1}^{2} e^{-2 i \sigma_{n} \tau_{n}^{j}}+\frac{m}{(1+\beta)^{2}} q_{1} q_{2} e^{-i \sigma_{n} \tau_{n}^{j}}} \gamma_{n}^{2},
\end{aligned}
$$

where $d \Delta$ and $L$ is defined in (2.3). Similarly $E_{2}$ is uniquely determined by

$$
\begin{aligned}
& -d \Delta E_{2}-L\left(E_{2}\right) \\
= & \binom{2\left(\frac{k-\beta}{k(1+\beta)^{2}}-\frac{1}{k}\right) q_{1} \bar{q}_{1}-\frac{m}{(1+\beta)^{2}}\left(q_{1} \bar{q}_{2}+\bar{q}_{1} q_{2}\right)}{-2 \frac{k-\beta}{k(1+\beta)^{2}} q_{1} \bar{q}_{1}+\frac{m}{(1+\beta)^{2}}\left(q_{1} \bar{q}_{2} e^{-i \sigma_{n} \tau_{n}^{j}}+\bar{q}_{1} q_{2} e^{i \sigma_{n} \tau_{n}^{j}}\right)} \gamma_{n}^{2} .
\end{aligned}
$$

Then we can easily obtain $E_{1}$ has the expression as $e_{1}+e_{2} \cos \frac{2 n x}{l}$ where $e_{1}, e_{2} \in \mathbb{C}^{2}$, and $E_{2}$ has the expression as $f_{1}+f_{2} \cos \frac{2 n x}{l}$ where $f_{1}, f_{2} \in \mathbb{C}^{2}$, and we omit the detailed computation. With these modifications, we are able to compute the direction of Hopf bifurcation in the more general situation where the diffusion term also plays a role.

Acknowledgments. The authors wish to thank the reviewers for their valuable comments and suggestions which greatly improved the presentation of this work.

## REFERENCES

[1] S. Chen, J. Shi and J. Wei, Global stability and Hopf bifurcation in a delayed diffusive LeslieGower predator-prey system, Int. J. Bifurcation Chaos., 22 (2012), 1250061.
[2] T. Faria, Normal forms and Hopf bifurcation for partial differential equations with delays, Trans. Amer. Math. Soc., 352 (2000), 2217-2238.
[3] T. Faria, Stability and bifurcation for a delayed predator-prey model and the effect of diffusion, J. Math. Anal. Appl., 254 (2001), 433-463.
[4] T. Faria and L. T. Magalh, Normal forms for retarded functional-differential equations with parameters and applications to Hopf bifurcation, J. Differential Equations., 122 (1995), 181200.
[5] T. Faria and L. T. Magalh, Normal forms for retarded functional-differential equations and applications to Bogdanov-Takens singularity, J. Differential Equations., 122 (1995), 201-224.
[6] B. C. Goodwin, "Temporal Organzization in Cells," Academic Press, London and New York, 1963.
[7] J. K. Hale, "Theory of Functinal Differentail Equations," Second edition. Applied Mathematical Sciences, 3. Springer-Verlag, New York-Heidelberg, 1977.
[8] B. D. Hassard, N. D. Kazarinoff and Y.-H. Wan, "Theory and Application of Hopf Bifurcation," Cambridge University Press, Cambridge-New York, 1981.
[9] C. S. Holling, Some characteristics of simple types of predation and parasitism, Canadian Entomologist, 91 (1959), 385-398.
[10] G. Hu and W. Li, Hopf bifurcation analysis for a delayed predator-prey system with diffusion effects, Nonl. Anal. Real World Appl., 11 (2010), 819-826.
[11] G. E. Hutchinson, Circular causal systems in ecology, Ann. N.Y. Acad. Sci., 50 (1948), 221246.
[12] W. Ko and K. Ryu, Qualitative analysis of a predator-prey model with Holling type-II functional response incorporating a prey refuge, J. Differential Equations., 231 (2006), 534-550.
[13] X. Lin, J. W.-H. So and J. Wu, Center manifolds for partial differential equations with delay, Proc. Roy. Soc. Edinburgh., 122 A (1992), 237-254.
[14] R. M. May, Limit cycles in predator-prey communities, Science, 177 (1972), 900-902.
[15] A. B. Medvinsky, S. V. Petrovskii, I. A. Tikhonova, H. Malchow and B.-L. Li, Spatiotemporal complexity of plankton and fish dynamics, SIAM Rev., 44 (2002), 900-902.
[16] R. Peng and J. Shi, Non-existence of non-constant positive steady states of two Holling typeII predator-prey systems: Strong interaction case, J. Differential Equations., 247 (2009), 866-886.
[17] M. L. Rosenzweig and R. MacArthur, Graphical representation and stability conditions of predator-prey interaction, Amer. Natur., 97 (1963), 209-223.
[18] S. Ruan and J. Wei, On the zeros of transcendental functions with applications to stability of delay differential equations with two delays, Dyn. Contin. Discrete Impuls. Syst. Ser. A Math. Anal., 10 (2003), 863-874.
[19] H. Thieme and X. Zhao, A non-local delayed and diffusive predator-prey model, Nonl. Anal. Real World Appl., 2 (2001), 145-160.
[20] P. K. C. Wang, Asymptotic stability of a time-delayed diffusion system, J. Appl. Mech. Ser., E 30 (1963), 500-504.
[21] Y. Wang, Asymptotic behavior of solutions for a class of predator-prey reaction-diffusion systems with time delays, J. Math. Anal. Appl., 328 (2007), 137-150.
[22] J. Wu, "Theory and Applications of Partial Functional-Differential Equations," Applied Mathematical Sciences, 119. Springer, New York, 1996.
[23] D. Xiao and S. Ruan, Multiple bifurcations in a delayed predator-prey system with nonmonotonic functional response, J. Differential Equations., 2001 (2009), 494-510.
[24] X. Yan, Stability and Hopf bifurcation for a delayed prey-predator system with diffusion effects, Appl. Math. Comput., 192 (2007), 137-150.
[25] X. Yan and C. Zhang, Asymptotic stability of positive equilibrium solution for a delayed prey-predator diffusion system, Applied Mathematical Modelling, 34 (2010), 184-199.
[26] F. Yi, J. Wei and J. Shi, Bifurcation and spatiotemporal patterns in a homogeneous diffusive predator-prey system, J. Differential Equations, 246 (2009), 1944-1977.
[27] J. Zhang, W. Li and X. Yan, Multiple bifurcations in a delayed predator-prey diffusion system with a functional response, Nonl. Anal. Real World Appl., 11 (2010), 2708-2725.

Received November 2010; revised April 2012.
E-mail address: chenshanshan221@gmail.com
E-mail address: shij@math.wm.edu
E-mail address: weijj@hit.edu.cn


[^0]:    2000 Mathematics Subject Classification. Primary: 35K57; Secondary: 35R10, 92D25.
    Key words and phrases. Predator-prey, delay, stability, Hopf bifurcation, periodic orbit.
    Shanshan Chen is supported by a grant from China Scholarship Council, Junping Shi is supported by NSF grant DMS-1022648 and Junjie Wei is supported by China-NNSF grants 11031002.
    ${ }^{1}$ Corresponding Author

